Pedobiologia **42**, 278–282 (1998)
Gustav Fischer Verlag Jena

Species composition, developmental stages and abundance of Pauropoda in coniferous forest soils of southeast Norway

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Accepted: 5. September 1997

Summary. Pauropoda were sampled during spring and autumn in two coniferous forest areas near Oslo, one above and one below the marine limit. In each area, seven different vegetation types were sampled, from the poorest pine forest soils to the richest spruce forest soils. Pauropoda were present only in the area below the marine limit, and furthermore restricted to medium rich and rich soils. One species (*Pauropus lanceolatus*) was only found in podzolic soil, while the other four species were found in brown earth soils (*Allopauropus gracilis, A. vulgaris, A. cuenoti* and *A. multiplex*). Highest densities in three of the species were in the richest soils with a high soil humidity (up to 3250 m^{-2} in *A. vulgaris*). While the abundance of *A. cuenoti* seemed to decrease with increasing depth down to 12 cm, *A. vulgaris* had the highest density in the 3–9 cm layers. Age distributions of these two species in the 0–6 and 6–12 cm layers were similar, indicating that reproduction was not restricted to certain depths. *A. vulgaris, A. cuenoti* and *A. gracilis* are believed to reproduce continuously during the warm season, since newly hatched individuals and various developmental stages were present both in spring and autumn. Males were generally rare, and it is believed that at least *A. cuenoti* is parthenogenetic in the nordic countries. It is suggested that further studies should include much deeper soil layers.

Key words: Pauropoda, species composition, developmental stages, abundance, soil types, coniferous forest

Introduction

The Pauropoda are usually overlooked in soil fauna studies. Their densities are generally low, and they are rarely identified to species level. The few records from Norway, resulting mainly from haphazard manual collecting from various habitats, have recently been summarized by Scheller (in press). That paper presents the known distribution of 13 species from 5 genera. Earlier, Leinaas (1974) studied two species in two coniferous forests in Akershus county, a study with an ecological touch.

The present results are part of a systematic study of the microarthropod fauna in various coniferous forest soils in SE Norway. While a separate paper has given the abundance and vertical distribution of Pauropoda, Protura and Symphyla on group level (Hågvar 1997), this paper analyses the Pauropoda material with respect to species and developmental stages. Such detailed studies are rare, and little is known about the ecology of each species.

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Materials and Methods

Detailed information about habitats, soil profiles and sampling has been given by Hågvar (1982). Samplings were performed in 1977–1978 at two localities in SE Norway: Skrukkelia, 60 km north of Oslo, situated above the marine limit (term for the upper sea level, last glaciation), and Ås, 30 km south of Oslo, situated below the marine limit. In both localities, 7 different vegetation types in coniferous forest were sampled, from the poorest pine forest soils to the richest spruce forest soils. A short version of site and soil descriptions has been given by Hågvar (1997). Pauropoda were found only in the locality below the marine limit, and only in the spruce forest habitats. These were, according to increasing soil fertility:

1. "Bilberry vegetation": Association *Eu-Piceetum Myrtillus*. Iron podzol, raw humus.
2. "Small ferns": Association *Eu-Piceetum Dryopteris*. Brown earth, raw humus.
3. "Small herbs": Association *Melico-Piceetum Typical*. Brown earth, mull humus.
4. "Tall herbs": Association *Melico-Piceetum Athyrium*. Brown earth, mull humus.
5. "Tall herbs, super": As above, but very rich soil.

A single sampling usually consisted of 20 soil cores to a depth of 12 cm, each covering 10 cm^2. The cores were divided into four vertical sections, each 3 cm deep. All sites were sampled both during spring (May) and autumn (August/September).

Results

Five species were recorded: *Pauropus lanceolatus* Remy, *Allopauropus gracilis* (Hansen), *A. vulgaris* (Hansen), *A. cuenoti* (Remy), and *A. multiplex* Remy. Table 1 shows the abundance of each species in the various vegetation types during spring and autumn. *P. lanceolatus* was only recorded in the podzol soil (bilberry vegetation) and was absent from the brown earths. All other species were restricted to brown earth profiles, i.e. to the richest soils and vegetation types. The highest abundance both totally and at species level was recorded at the richest site in spring: 4110 totally m^{-2} , and 3250 m^{-2} of *A. vulgaris*. There could be considerable differences in abundance of a given species between spring and autumn samplings, and in most cases the spring abundance was highest.

Due to low individual numbers (cf. Table 3), the vertical distribution has been calculated only for *A. vulgaris* and *A. cuenoti*, pooling data from all samplings (Table 2). *A. vulgaris* showed a maximum between 3 and 9 cm depth, with a minimum in the upper 3 cm. The

Table 1. Number of Pauropoda m^{-2} in different vegetation types and seasons. Only autumn samples exist from bilberry vegetation. s.= spring, a.= autumn. Full names of genera are *Pauropus* and *Allopauropus*

Vegetation type	Bilberry	Small ferns		Small herbs		Tall herbs		Tall herbs, "super"	
Season	*a.*	*s.*	*a.*	*s.*	*a.*	*s.*	*a.*	*s.*	*a.*
P. lanceolatus	1780								
A. gracilis		50	150	240	50	210	50	530	180
A. vulgaris		1210	50			310	930	3250	470
A. cuenoti		210				1240	760	330	
A. multiplex							50		
Total Pauropoda	1780	1470	200	240	50	1760	1790	4110	650

Table 2. Vertical distribution of *Allopauropus vulgaris* and *A. cuenoti*, based on 103 and 47 specimens, respectively

Depth (cm)	*A. vulgaris* (%)	*A. cuenoti* (%)
0–3	7	39
3–6	38	28
6–9	39	24
9–12	17	9

Table 3. Distribution of developmental stages in each species at spring and autumn samplings. Pooled data from all localities. N = number of individuals identified. s. = spring, a. = autumn. The developmental stages are explained in the text

Developmental stage	Juv. 3	Juv. 5	Juv. 6	Subad. 8♀	Subad. 8♂	Ad. 9♀	Ad. 9♂	Ad. 10♀	N
A. vulgaris (s.)	28	4	8			33	4		77
A. vulgaris (a.)	9		4		1	12			26
A. cuenoti (s.)	6	8	3	5		6		5	33
A. cuenoti (a.)	7	2	2			2		1	14
A. gracilis (s.)	2	1	9	1		3			16
A. gracilis (a.)	2		2			3			7
A. multiplex (a.)	1								1
P. lanceolatus (a.)	2	3	4	1		2	1		13

Table 4. Distribution of developmental stages in 0–6 cm and 6–12 cm depth for the two most abundant species. Pooled samples from all vegetation types and seasons. The developmental stages are explained in the text

Developmental stage		Juv. 3	Juv. 5	Juv. 6	Subad. 8♀	Subad. 8♂	Ad. 9♀	Ad. 9♂	Ad. 10♀	N
A. vulgaris	0–6 cm	16	4	2			21	3		46
A. vulgaris	6–12 cm	21		10		1	24	1		57
A. cuenoti	0–6 cm	9	8	3	4		6		1	31
A. cuenoti	6–12 cm	4	2	2	1		2		5	16

limited data from *A. cuenoti* indicates a decreasing abundance with increasing depth. Both species are probably found deeper than 12 cm. Also *A. gracilis* was found in all four vertical layers. The bilberry sampling where *P. lanceolatus* was found was taken only down to 6 cm, and the species was present in about equal numbers in both layers. Only one individual of *A. multiplex* was found, in the upper 3 cm.

Pauropoda go through the following developmental stages: Juveniles with 3, 5 and 6 pairs of legs, subadults with 8 pairs, and adults with 9 or 10 pairs of legs. The sex can be identified from subadults on, but only females may achieve 10 pairs of legs. Table 3 sums up the distribution of developmental instars in each species, based on pooled material from all vegetation types. The main conclusion is that a mixture of developmental stages, from newly hatched to adults, may be found both in spring and in autumn. Males were rare, and only documented in *A. vulgaris* and *P. lanceolatus*.

In the two most abundant species, the distribution of developmental stages has been compared in two vertical layers: 0–6 cm and 6–12 cm depth (Table 4). There was a mixture of developmental stages in both layers, and no indication that adults and juveniles prefer different depth levels.

Discussion

The complete absence of Pauropoda in the locality 60 km north of Oslo, where the whole range of coniferous forest types was present, is remarkable. This locality is colder, has a longer winter period and lacks marine sediments (Hågvar 1982). However, other records from the Holarctic do not indicate that these factors should exclude Pauropoda. This animal group often shows a patchy distribution, and we take this case as an example of the unpredictability of the Pauropoda fauna. The general absence in poor pine forest soils and the limitation to mull soils in four of the five species (Table 1) point to a preference for rich spruce localities within Norwegian coniferous forests. The limitation of *P. lanceolatus* to bilberry forest with

raw humus may be due to its large size (1.5 mm), being favoured by a loose raw humus structure. Leinaas (1974) also found this species in raw humus soil, and even up in the moss vegetation. He recorded a mean density of 600 m^{-2} throughout the year, varying from 0 to 1600 m^{-2}, thus approaching the present value of 1780 m^{-2}.

In Sweden, three of the *Allopauropus* species from the present study have been recorded in agricultural soils: *A. gracilis, A. vulgaris* and *A. cuenoti* (Lagerlöf & Scheller 1989). Over a broader geographical range, the five recorded species have been reported in various soil types, and they may inhabit the litter layer as well as the mineral soil, sometimes to great depth (Scheller, in press). Their flexibility is furthermore reflected through their wide distribution (Scheller, in press): *A. gracilis* may be subcosmopolitan. *A. vulgaris* is very common in the West Palearctic and Nearctic, and is known also from Africa and South Asia. *A. cuenoti* is mainly a West Palearctic species but is known also from Africa and Canada. In Europe, it is more common in the north than in the south. *A. multiplex* is a rare species which has been found in the West Palearctic and Canada. In Norway, it has been found only in one other locality. *P. lanceolatus* has earlier been confused with *P. huxleyi* Lubbock, so its range cannot be given. However, it may cover wide areas in the Holarctic. Within Norway, Sweden, Finland and Denmark, it has been found only in a few localities. While it appeared only in podzolic soil in the present study, it has elsewhere been recorded in brown earth sites as well.

Tables 1–2 indicate the following differences between the species, as far as Norwegian coniferous forests are concerned:

P. lanceolatus may be a podzol soil species, while the other ones are brown earth species. *A. multiplex* is very rare, while *A. vulgaris* is often rather abundant. *A. vulgaris* may live somewhat deeper than *A. cuenoti*. Probably, the species are to a certain degree ecologically segregated, even though their great geographical distribution and occurrence in many soil types may give the impression that they are all generalists.

A survey of the Pauropoda in some Austrian forests indicated a positive correlation between abundance and sufficient soil moisture (Meyer & Scheller 1992). The two richest vegetation types (tall herbs and tall herbs „super"), which gave the highest abundance values of three of the present species, were also the two sites with highest soil moisture. A general high abundance in the spring of the same three species may be due to high soil moisture after snow melt. In further studies on vertical distribution of Pauropoda species, soil moisture should be included as a possible regulating factor.

While we refer to Hågvar (1997) for a general discussion on total densities of Pauropoda, we note that very few investigations exist on population densities of Pauropoda in northern forests. Furthermore, there is an almost complete absence of studies dealing with the ecology and life cycle of single species. In the present study, great care was taken to pick out even the smallest stages from the samples, and to identify all specimens to stage. Since the first stage, which lasts only a very short time, occurs both in spring and autumn (upper three species in Table 3), we suggest that the reproductive period lasts for the whole warm part of the year. This is supported by various samplings of Pauropoda in Scandinavia by Scheller (unpubl.), where Juv. 3 has been taken from June to October, and Juv. 5 and 6 from early May to the middle of November.

In *P. lanceolatus*, Leinaas (1974) likewise found all developmental stages present throughout the year. Also from Austrian forests, Meyer & Scheller (1992) concluded that *A. vulgaris* and *A. gracilis* bred continuously from spring to autumn, but speculated that *A. cuenoti* might be a spring breeder. Our data show that it may reproduce even in the autumn.

In contrast with Symphyla, where Edwards (1959, 1961) found that egg-laying took place in deeper layers, Pauropoda probably reproduce in all vertical layers. We failed to find clear differences in age distribution between 0–6 and 6–12 cm layers (Table 4).

Males were rare, and only found in two species: *A. vulgaris* and *P. lanceolatus* (Table 3). At least *A. cuenoti* seems to be a parthenogenetic species in the nordic countries. No males have been found of *A. cuenoti* in Norway, Sweden, Finland or Denmark, but males occur in more southern countries, such as France, Germany and Switzerland (Scheller, unpubl.). Some

tropical-subtropical species are also probably parthenogenetic, since males have never been seen, even within large samples (Scheller 1970).

Further nordic studies on Pauropoda should include sampling from much deeper layers. It is known that Pauropoda may live at a depth of more than one metre, and deep layers may contain additional species which are not discovered through ordinary sampling.

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